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Summary of phylogeny in subfamily Colobinae (Primate: Cercopithecidae)

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The phylogeny of the colobine monkeys has a complex evolutionary history, evolving several distinct radiations and owned a wide range of forest and woodland habits in tropical Africa and in southern and eastern Asia. Understanding the true evolutionary history of the colobine monkeys becomes an important field and has received special attention. In this article, we review phylogeny of Colobinae based on previous fossil, cytological, morphological and molecular evidence and indicate the phylogenetic controversies. This review is expected to guide the future research of Colobinae phylogeny, and also provide theoretic evidence for the conservation of these highly endangered and unique primates.

Colobinae, phylogeny, Asian presbytina, African colobinae

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The Old World monkeys consist of two living subfamilies —the cheek-pouch monkeys (Cercopithecinae) and the leaf-eating monkeys (Colobinae) [1], both of which are the closest living relatives to the apes (Hominoidea) (Figure 1) [1], but previous studies had focused on Cercopithecine evolution as a model for human evolution history. The phylogenetic and evolution of the leaf-eating monkeys (Colobinae), on the other hand, had been a relatively neglected issue. In these years, the colobine monkeys, especially Asian colobines, are facing extinction because of the increasing deforestation and hunting rates by people. Therefore, it is necessary for us to promote the conservation of these highly endangered and unique primates.

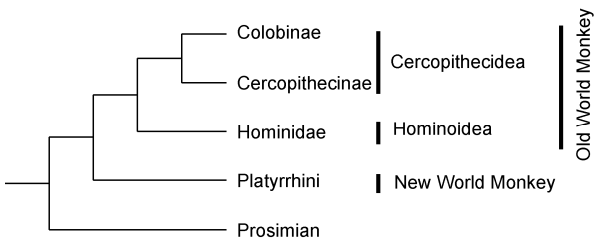

Figure 1 The phylogeny of main families in primates.

Compared with Cercopithecinae, the colobine monkeys have a sharp-cusped cheek teeth and relatively narrow incisors [2]. Their dimensions vary from 4 kg in the African olive colobus (*Procolobus verus*) to 20 kg of the adult males of the proboscis monkey in Borneo (*Nasalis larvatus*). They are characterized by the very short and in some case degraded thumb. The hind legs are usually longer than the front legs. Most of the species have no cheek pouch outside, and have very long tail except the pig-tailed langur (*Simias concolor*) [3].

Besides the features as described above, the subfamily Colobinae has evolved a complex ruminant-like stomach and foregut in which microbes ferment these indigestible plant materials [4], leading to their unique adaptation to the

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leaf-eating feeding habits [5–8]. In view of this, the Colobinae has also been the crucial model animals for the study of the molecular mechanisms of adaptive evolution [9,10]. The pancreatic ribonuclease gene (*RNASE*) duplication has been believed to be closely related to the adaptation of Colobines to the unique leaf-feeding lifestyle [5–8]. While all of the other primates have only one *RNASE1* gene, multiple *RNASE1* genes have been intriguingly observed in Colobines, evolving rapidly under positive selection for enhanced digestive efficiencies, as an adaptive response to the increased demands for the enzyme for digesting bacterial RNA (Figure 2).

The colobines consist of 10 genera in two subtribes— the African Colobina (including the genera *Colobus*, *Piliocolobus*, and *Procolobus*) and the Asian Presbytina (including the genera *Pygathrix*, *Rhinopithecus*, *Nasalis*, *Simias*, *Presbytis*, *Trachypithecus* and *Semnopithecus*) [1,11–14]. Based on fossil records, the divergence between ancestral African colobines and Asian colobines was estimated between 10 [15] and 13 Ma [16]. The colobines not only experience recent and rapid adaptive radiations, but also are more diverse and widespread for different climate environments [12]. In view of this, the phylogeny of the colobine monkeys has a complex evolutionary history, evolving several distinct radiations and owned a wide range of forest and woodland habits in tropical Africa and in southern and eastern Asia. Understanding the true evolutionary history of the colobine monkeys, therefore, becomes an important field and has received special attention. However, due to the fact that nearly all the extant colobine genera diversify from one another within a four-million-year window [17–19], attempts to clarify relationships among these colobine genera have encountered challenges.

In this article, we review the phylogeny of the colobine monkeys based on previous fossil, morphological physiology, cytology and molecular evidences, and indicated the phylogenetic controversies. This review is expected to shed light on the research of Colobinae phylogeny and adaptive evolution, and also provide a theoretical foundation for the conservation of these highly endangered and unique primates.

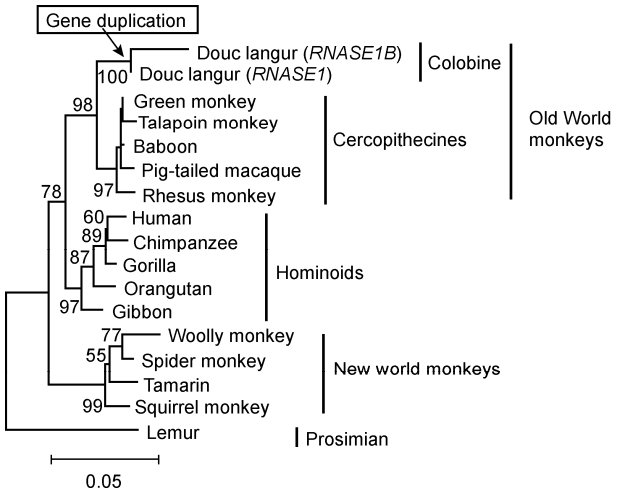

Figure 2 The unique duplication of *RNASE1* gene in Colobines compared with other primates [5].

1 Phylogeny of African Colobinae

The diversification of African colobines, which distributed across the African rainforest belt, represented a major component of African primate evolution [20,21]. According to fossil records, the earliest African colobines were found in the late Miocene about 8.5−9 Ma [22].

African colobines include three genera, i.e., *Colobus* (black-and-white colobus), *Procolobus* (olive colobus), and *Piliocolobus* (red colobus) [20,23]. *Colobus* diverged first, and followed by the progenitor of *Piliocolobus* and *Procolobus* [17,19,24–26]. Based on both morphology and genetics evidence, it was well-recognized that *Procolobus* was the sister-taxon of (and possibly congeneric to) *Piliocolobus* [12,19,24,26–28]. In other words, there was a general consensus for the more close relationship between *Piliocolobus* and *Procolobus* within African colobines.

In earlier analyses of morphological and molecular data, all supported that the African colobine forms a monophyletic clade [1,12,19], grouping *Piliocolobus*, *Procolobus*, and *Colobus* together [17–19,24–26,29,30] (Figure 3). Interestingly, a recent phylogenetic analyses of 83 mobile elements from Roos et al. [19] indicated a closer association of the *Procolobus*/*Piliocolobus* clade to Asian colobines than to *Colobus*, a relationship that was not rejected by nuclear sequence data in their study, leading them to propose African colobines paraphyly hypothesis (Figure 3(e)). This finding thus challenged the traditional view of the monophyly of African colobines. An ancient hybridization between *Colobus* male and *Procolobus*/*Piliocolobus* females had been proposed by them to explain their new finding. However, a most recent study of Wang et al. [31] supported the traditional view of the monophyly of the African colobines based on 44 nuclear non-coding genes and the whole mt genome (Figure 3(d) and (g)).

2 Phylogeny of Asian Presbytina

Compared with African colobinae, Asian Presbytina has more diverse members and wider geographic distribution [1,12]. The classification of Asian genera varies from 3 to 9 genera based on previous studies. Groves [32] and Grzimek [33] classified Asian colobines into three genera: *Presbytis*, *Pygathrix*, and *Nasalis*; Elliot [34] divided them into 4 genera: *Pygathrix*, *Rhinopithecus*, *Nasalis*, and *Simias*. Macdonald [35] also recognized 4 genera, but referred as *Presbytis*, *Semnopithecus*, *Pygathrix*, and *Nasalis*. In comparison,

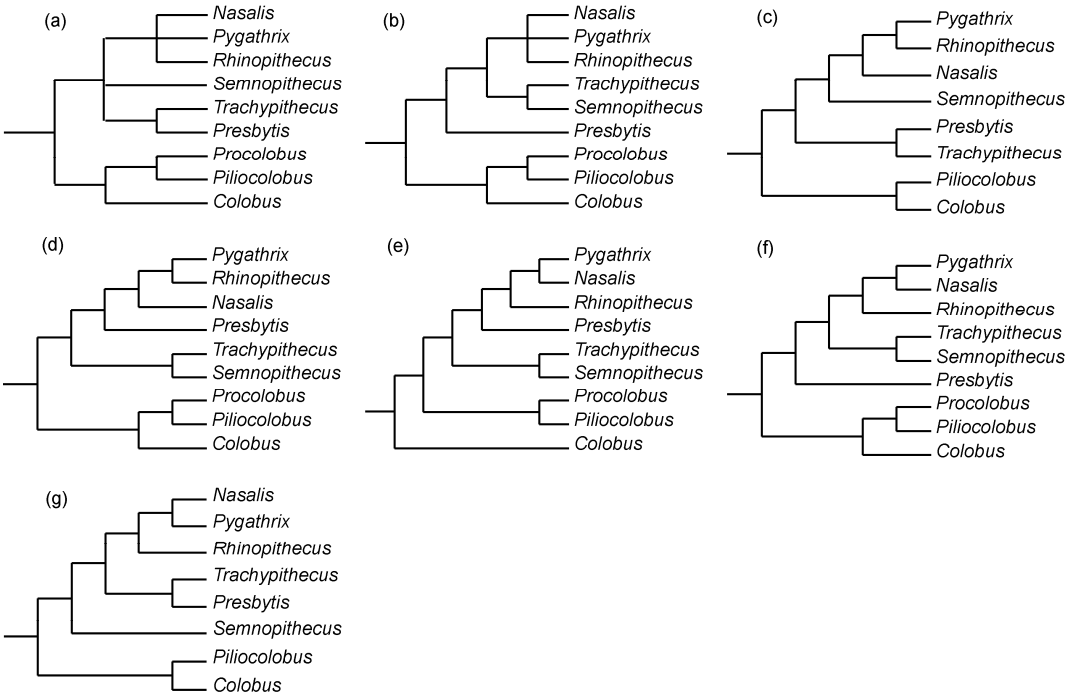

Figure 3 Hypotheses of phylogenetic relationships among Colobine genera. Trees were reconstructed based on (a) 12 protein-coding mt genes (10 kb) [17]; (b) fragment of X-chromosome (4.3 kb) [26] and 54 nuclear genes (35 kb) [18]; (c) complete *cytb* gene (1.8 kb) [30] and 7 mt genes (6.1 kb) [29]; (d) 15 mt genes and 43 nuclear genes (42 kb) [25], 44 nuclear non-coding genes (23 kb) [31]; (e) 83 mobile elements [19]; (f) nuclear genes (13 kb) [19]; (g) complete mt genomes (16.5 kb) [31].

Napier and Napier [36], Simpson [37], and Ellerman et al. [38] grouped the Asian colobines into five genera: *Presbytis*, *Pygathrix*, *Rhinopithecus*, *Nasalis*, and *Simias*, while Hershkovitz [39] and Nowak [40] proposed seven genera: *Presbytis*, *Semnopithecus*, *Trachypithecus*, *Pygathrix*, *Rhinopithecus*, *Nasalis*, and *Simias*. Hill [41–43] classified them into 9 genera: *Presbytis*, *Semnopithecus*, *Trachypithecus*, *Pygathrix*, *Rhinopithecus*, *Nasalis*, *Simias*, *Kasi* and *Prebyticus*. In recent years, there was a consensus that the Asian colobines were referred as langurs and comprised of 7 genera, i.e., *Semnopithecus*, *Trachypithecus*, *Presbytis*, *Pygathrix*, *Rhinopithecus*, *Nasalis* and *Simias* [1,12,14, 44,45]. In addition, these 7 genera were clustered into 2 groups, i.e., the odd-nosed monkey group (including *Pygathrix*, *Rhinopithecus*, *Nasalis* and *Simias*) and the langur group (including *Presbytis*, *Trachypithecus* and *Semnopithecus*) [46–48].

Asian colobines represent a typical example of an evolutionary radiation with rapid diversification events that date back to Middle Miocene about 10–15 Ma [11,12]. Therefore, phylogenetic relationships within Asian colobines, including those among genera and some species had been disputed hotly in previous studies and were not well established yet [1,17–19,25,26,29–31,49–59].

2.1 Intergeneric relationships within Asian Presbytina

(i) Phylogeny of the odd-nosed monkey group. Though the monophyly of the odd-nosed monkey group has been unambiguously established from previous studies of both morphology and geographical distribution [1,11,12,14,60] and confirmed by genetic data [17–19,26,30,31,52], there had long been controversy over the relationships among the genera within this group. It was especially the case that among *Pygathrix*, *Rhinopithecus* and *Nasalis* (Figure 3) [17–19,26,30,31,48].

Based on the previous morphological studies, Grove [46] and Delson [61] favored the association of *Pygathrix* and *Rhinopithecus* to the exclusion of *Nasalis* and this was congruent with molecular evidences based on the analyses of mitochondrial (mt) *ND3-ND4* (2.2 kb), *12SrRNA* (387 bp) genes by Wang et al. [49], and Li et al. [51], whereas Jablonski et al. [47,48,55] grouped *Nasalis* with *Pygathrix* to the exclusion of *Rhinopithecus* by combining fossils and 455 characters of morphological data. Zhang et al. [50] analyzed mt *cytb* gene fragment (424 bp) and support the sister-grouping of *Nasalis* and *Rhinopithecus* to the exclusion of *Pygathrix*. More recently, further efforts had been undertaken to obtain phylogenetic relationships using large datasets from mt genomes and nuclear genes. In the studies of Chatterjee et al. [29] (6.1 kb), Fabre et al. [25] (42 kb) and Meyer et al. [30] (1.8 kb), as well as Wang et al. [31] (23 kb), all of which were conducted based on mt or nuclear sequence data, a sister-taxon association between *Pygathrix* and *Rhinopithecus* were consistently indicated (Figure 3(c) and (d)), whereas the studies of Roos et al. [19] and Wang

et al. [31] supported a close association of *Pygathrix* with *Nasalis* to the exclusion of *Rhinopithecus* based on both 83 mobile elements (Figure 1(e)) and nuclear genes (13 kb) (Figure 3(f)) as well as the whole mt genomes (16.5 kb) (Figure 3(g)). Furthermore, Sterner et al. [17], Ting et al. [26] and Perelman et al. [18] also attempted to resolve the relationships among *Pygathrix*, *Rhinopithecus*, and *Nasalis* within the odd-nosed monkeys based on mt protein-coding genes (10 kb) (Figure 3(a)), X-chromosome (4.3 kb), and nuclear genes (35 kb) (Figure 3(b)), respectively, but the three genera formed a polytomy.

In comparison, when it came to the phylogenetic position of *Simias* in the odd-nosed monkey group, the debate on its systematic placement appeared remarkably subdued because all previous morphological and molecular analyses supported it as the sister-taxon (and possible subgenus) to *Nasalis* [19,61,62], with the exception of a recent study of 7 mitochondrial (mt) gene fragments (6.1 kb) from Chatterjee et al., [29] in which *Simias* had a closer relationship with *Pygathrix*/*Rhinopithecus* than *Nasalis*.

(ii) Phylogeny of the langur group. Another area being in hot dispute comes from the relationships between the langur genera and the odd-nosed monkey group. In fact, there has long been debate about the determination of three genera within the langur monkey group in earlier studies. *Semnopithecus*, and *Trachypithecus* had been ever grouped into *Presbytis* as one genus [46,63–66]. In comparison, more evidence separated *Trachypithecus* from *Presbytis*, including those from Oate et al. [67] and Brandon-Jones et al. [14] based on ecological and morphological data, as well as Md-Zain etc. based on mt *ND3*, *ND4L*, *ND4* (2.3 kb) [68] and *COII* (850 bp) [69] genes. Hill [43] and Hooijer [70] subdivide the genus *Presbytis* into *Semnopithecus* and *Trachypithecus* subgenus. In addition, *Trachypithecus* had also been formerly considered as a subgenus of *Semnopithecus* [16,27,71,72].

Recent studies provided contradicting relationships between these three langur genera and the odd-nosed monkey group (Figure 3). Growing studies are supporting the non-monophyly of the langur monkey group.

Sterner et al. [17] suggested a sister-group between *Presbytis* and *Trachypithecus* within the langur group, but failed to resolve the relationships among *Presbytis*/*Trachypithecus*, *Semnopithecus*, and the odd-nosed monkey group based on 12 mt protein-coding genes (10 kb) of 6 Asian colobine genera (Figure 3(a)). Ting et al. [26] claimed that *Presbytis* diverged earliest, followed by the split between *Trachypithecus*/*Semnopithecus* and the odd-nosed monkey group within the Asian colobines by examining a fragment of the X-chromosome (4.3 kb) (Figure 3(b)). The results were congruent with the study by Perelman et al. [18] including ~35 kb genome sequences from 54 nuclear genes of 186 primates. In contrast, both Chatterjee et al. [29] and Meyer et al. [30] favored the earliest divergence of *Presbytis*/*Trachypithecus* within Asian colobinae, and the close relatedness of *Semnopithecus* and the odd-nosed monkey group based on the analyses of 7 mt genes (6.1 kb) and a fragment of mt genes (1.8 kb) (Figure 3(c)), but they lacked significant supports. Fabre et al. [25] analyzing combined mt and nuclear genes (42 kb), and Wang et al. [31] analyzing 44 nuclear non-coding genes (23 kb), both found support for close relationships between *Trachypithecus* and *Semnopithecus*, and between *Presbytis* and the odd-nosed monkeys (Figure 3(d)). These same relationships were also confirmed by Roos et al. [19], who performed an analysis of 83 mobile elements (Figure 3(e)). Moreover, they also supported the former *Semnopithecus*/*Trachypithecus* clade, but suggested *Presbytis* as sister to the other Asian colobines based on nuclear genome data analyses (13 kb) (Figure 3(f)). However, by analyzing the whole mt genome (16.5 kb), Wang et al. [31] proposed that *Semnopithecus* diverged earliest, followed by the split between *Trachypithecus*/*Presbytis* and the odd-nosed monkey group within the Asian colobines (Figure 3(g)).

The results from the above studies demonstrated that the relationships among langur monkey group and odd-nosed monkey group remain unresolved, although hybridization had been raised for a most likely explanation for some of these incongruent relationships [19,73].

2.2 Interspecies relationships within Asian Presbytina

(i) Interspecific relationships in genus *Rhinopithecus*. The snub-nosed monkey genus *Rhinopithecus* is comprised of four distinct allopatric species [1,74]: *R. brelichi* (the gray snub-nosed monkey), *R. bieti* (the black snub-nosed monkey), *R. roxellana* (the golden snub-nosed monkey) and *R. avunculus* (the Tonkin snub-nosed monkey). Except for *R. avunculus*, which is distributed in low-altitude subtropical forests in northwestern Vietnam [75], the other three *Rhinopithecus* species are endemic to temperate areas of China and inhabit six isolated high-altitude mountainous regions [76].

The phylogenetic relationships among the four *Rhinopithecus* species had all along been focusing issues. As seen from Figure 4, contradictory conclusions had been reached under different analyses. Zhang and Ryder [77] and Wang et al. [31] supported the sister group of *R. avunculus* and *R. bieti* to the exclusion of *R. roxellana* by analyzing mt *cytb* genes (253 bp) and 44 nuclear non-coding genes (23 kb), respectively (Figure 4(a)). Intriguingly, both Zhang and Ryder [50] and Li et al. [51] failed to resolve the phylogenetic relationships among *R. bieti*, *R. roxellana* and *R. avunculus* based on mt $tRNA^{Thr}$/*cytb* genes (424 bp) (Figure 4b) and mt *cytb* genes (402 bp) (Figure 4(c)), respectively, but *R. brelichi* was supported to diverge earlier than the other three species in the latter study (Figure 4(c)). Interstingly, different from Zhang et al. [50], in which mt $tRNA^{Thr}$/*cytb* genes were analyzed using MP and ML methods, Whittaker et al. [62] analyzed these two genes

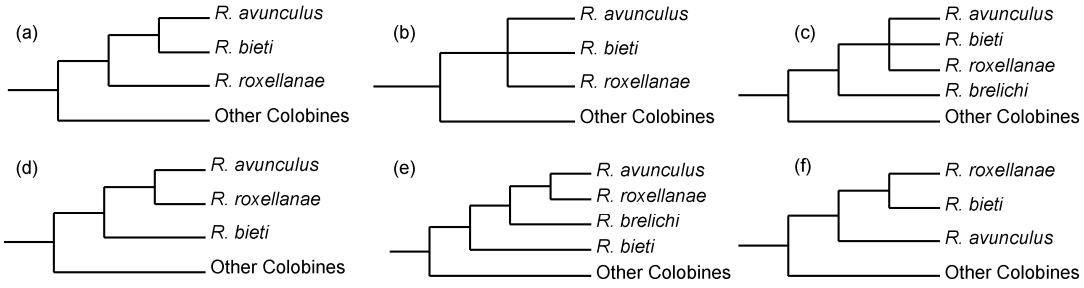

Figure 4 Hypotheses of phylogenetic relationships among four species of the genus *Rhinopithecus*. Trees were reconstructed based on (a) fragment of mt *cytb* gene (253 bp) [77], 44 nuclear non-coding genes (23 kb) [31]; (b) fragment of mt $tRNA^{Thr}$/*cytb* gene (424 bp) [50]; (c) fragment of mt *cytb* gene (402 bp), mt 12S rRNA gene (387 bp) [51]; (d) fragment of mt $tRNA^{Thr}$/*cybt* gene (424 bp) [62]; (e) 15 mt genes and 43 nuclear genes (42 kb) [25], 7 mt genes (6,1 bp) [29]; (f) complete mt genomes (16.5 kb) [31].

using Bayesian method and supported the close relationship between *R. roxellana* and *R. avunculus* to the exclusion of *R. bieti* (Figure 4(d)). This relationship was also supported by Fabre et al. [25] and Chatterjee et al. [29], which utilized 15 mt and 43 nuclear genes (42 kb) (Figure 4(e)), as well as 7 mt fragment (6.1 kb) (Figure 4(e)), respectively. Interestingly, both Fabre et al. [25] and Chatterjee et al. [29] claimed the earliest divergent species among the genus *Rhinopithecus* group was *R. bieti* with significant support (Figure 4(e)), which was different from Li et al. [51] (Figure 4(c)). Recently, using the whole mt genome (16.5 kb), Wang et al. [31] supported the sister relationship between *R. roxellana* and *R. bieti* to the exclusion of *R. avunculus* (Figure 4(f)).

(ii) Interspecific relationships in genus *Trachypithecus*. *Trachypithecus* is the largest and most diverse genus of Asian Presbytina with a widest distribution, ranging from South India and Sri Lanka through mainland Southeast Asia to the Sundaland [52]. Within genus *Trachypithecus*, one species that had long been considered hard to determine phylogenetically is *T. pileatus* (the capped langur). Up to now, there were two conflicting hypotheses based upon previous analyses of mt *cytb* gene and two nuclear genes concerning the phylogenetic position of *T. pileatus*. Studies of partial mt genes clustered it with *Semnopithecus* [29,52,78,79]. However, nuclear gene based on Y chromosomal data and retroposon integrations analyses grouped it with *Trachypithecus* [52]. The remarkable discrepancy between mt and nuclear gene trees had led Osterholz et al. [52] and Karanth [80] to predict that *T. pileatus* might be the result of an ancient hybridization event between *Semnopithecus* and *Trachypithecus*. Additional information from mt and nuclear genomes should be added to resolve the enigmatic phylogenetic position of *T. pileatus* in the future studies.

Besides *T. pileatus*, the classifications and phylogenetic positions of *T. johnii* and *T. vetulus* had also been subjects of controversies in previous studies. In earlier studies, they were advised to be placed in their own genus *Kasi* due to their significant distinction from other species [42]. The subsequent analyses from the characters of cranial morphology, neonatal pelage color and sexually dichromatic pubic integument all classified them within *Trachypithecus* [14,40,45], whereas the growing molecular data clustered them within *Semnopithecus* [18,29,31,50,52,62,79], leading to the proposal that they should be reclassified to be *S. johnii* and *S. vetulus*.

3 Perspectives

The phylogeny of colobine monkeys, which are characterized by rapid species radiations and short internal tree branches, has long been one of the most plaguing and challenging problems in species tree reconstruction [81–83]. Up to now, only the monophyly of the odd-nosed monkey group had been unambiguously accepted. Main controversies were concentrated on (1) the paraphyletic or monophyletic origin of African colobina, (2) the intergeneric relationships among the Asian colobines genus, (3) the interspecific relationships within the odd-nosed monkeys group, and (4) the precise placement of *T. pileatus*.

Therefore, finding valid genetic markers that offer sufficient variation to distinguish among the recently divergent Colobinae species posed a major challenge to advancing the understanding of Colobine phylogeny. Earlier investigations of Colobinae phylogeny mainly utilized analysis of portions of a single or a small number of mt genes [49–52]. Recently, more efforts had been made to obtain the phylogenetic tree using large dataset from mt genomes and multiple nuclear genes [17–19,25,26,29–31]. However, many relationships within Colobinae remained a polytomy, evidence from additional characters were thus necessary to resolve them in the future study.

As the increasing availability of genomic data of more species, phylogenetic analysis is entering a new era—Phylogenomics, which use genomic data to infer evolutionary relationships [84]. By performing phylogenomic study, we are most likely to reconstruct a reliable phylogenetic tree using much more characters than those in previous studies, including gene families, large insertion and deletion gene fragments, and gene rearrangement [85–87]. These charac-

ters might be useful for distinguishing nodes resulting from rapid radiation episodes such as the Asian colobinae speciation events.

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